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ABSTRACT: Metabolizable energy requirements of the ewe increase during pregnancy due to increases in fetal and maternal metabolism. Fetal metabolism is related to total weight of the fetuses. Fetal number is a primary contributor to fetal weight. Litter birth weight represents the culminated fetal growth of the litter and can be used to estimate the effect of fetal metabolism on energy requirements of the ewe. We hypothesized that litter weight in sheep would increase at a decreasing rate with increasing litter size. Birth weights of lambs born to yearling (11 to 15 mo) and mature ewes (>34 mo) were collected on litters born to Dorset, Rambouillet, Suffolk, Finnsheep, Romanov, and Composite III ewes mated to produce straightbred lambs. Litter birth weight expressed as a function of litter size increased at a decreasing rate and the quadratic term differed from zero for mature Rambouillet, Suffolk, Finnsheep, Romanov, and Composite III litters ($P <$ 0.042). The quadratic coefficient differed among breeds. In yearlings, litter weight increased at a decreasing rate for Suffolk ewes ($P = 0.002$). The quadratic term for the relationship between litter weight and litter size did not differ from zero for Finnsheep ($P = 0.39$) or Romanov litters ($P = 0.07$). The hypothesis that litter weight increases at a decreasing rate with increased litter size is supported by experimental results.

Key Words: Breed, Ewe, Litter

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Introduction

Metabolizable energy requirements for ewes with a single fetus increase 50% above maintenance during late pregnancy (Rattray et al., 1974). This increase is even greater in ewes that have multiple fetuses. The increased energy requirements result from energy deposition in the conceptus (Rattray et al., 1974), energy used to support conceptus metabolism (Bell et al., 1987a), and energy used by maternal tissues to support the conceptus (Freetly and Ferrell, 1997). Approximately 60% of the increase in energy expenditure during pregnancy can be contributed to the gravid uterus and the remaining 40% to increased maternal metabolism (Freetly and Ferrell, 1997). During pregnancy, maternal metabolism changes to support the gravid uterus, and the timing of these changes is a function of both gestational length and fetal number (Freetly and Ferrell, 1998). Predicting nutrient requirements of ewes requires a knowledge of the dynamic nature of fetal metabolism during pregnancy. It has been well documented that birth weights of lambs decrease as litter size increases; however, less attention has been given to the relationship between litter size and litter birth weight. In swine, litter birth weight is positively correlated to litter size and pig birth weight is negatively correlated to litter size (Omtvedt et al., 1966). Conventional sheep production systems typically have used sheep breeds that give birth to one or two lambs. However, sheep breeds with greater prolificacy have been integrated into production systems. To estimate the maternal nutrient requirement, the relationship between litter weight and litter size needs to be established. We hypothesized that litter weight in sheep increases at a decreasing rate with increasing litter size. The objective of this study was to determine the relationship between litter birth weight and litter number of six breeds of sheep.

Materials and Methods

Sheep were maintained as resource flocks at the U.S. Meat Animal Research Center and their care complied with the *Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching* (FASS, 1999).

Litter birth weights of lambs born in 1992 through 2002 were collected in the months of December through June. Litters (n = 2,399) from six breeds of mature ewes (>34 mo, n = 1,726) were investigated. Those breeds were Dorset, Rambouillet, Composite III (a three-breed

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Table 1. Litter sizes of mature and yearling ewes

Age/breed	Litters, No.	Range in litter size	Litter size[a]
Mature ewes (>34 mo)			
Dorset	231	1 to 3	1.77 ± 0.04
Rambouillet	321	1 to 3	1.57 ± 0.03
Composite III[b]	684	1 to 4	1.87 ± 0.02
Suffolk	569	1 to 4	1.95 ± 0.02
Finnsheep	397	1 to 5	2.66 ± 0.04
Romanov	197	1 to 6	3.57 ± 0.07
Yearlings ewes (11 to 15 mo)			
Dorset	127	1 to 2	1.10 ± 0.03
Rambouillet	—	—	—
Composite III[b]	572	1 to 2	1.16 ± 0.02
Suffolk	313	1 to 3	1.22 ± 0.02
Finnsheep	437	1 to 4	1.74 ± 0.03
Romanov	80	1 to 4	2.49 ± 0.08

[a]Mean ± SEM.
[b]Composite III (a three-breed composite: ¼ Suffolk, ¼ Hampshire, ½ Columbia).

composite: ¼ Suffolk, ¼ Hampshire, ½ Columbia), Suffolk, Finnsheep, and Romanov. Litters from yearling ewes (11 to 15 mo) of the same breeds (minus Rambouillet) were also studied (n = 1,529). All litters consisted of straightbred lambs (Table 1).

Data were initially analyzed separately for each breed to establish whether a nonlinear relationship between litter birth weight and litter size existed. If maximum litter size within breed and age exceeded twins, then litter weight was regressed on litter size using the general quadratic model:

$$\text{litter weight} = f(x) = b_2x^2 + b_1x + b_0$$

where x = litter size. Data were analyzed using the GLM procedures of SAS (version 6.1, SAS Inst., Inc., Cary, NC). The probability that b_2 differs from zero was tested ($P < 0.05$). However, if b_2 did not differ from zero, we did not reject the null hypothesis and the relationship was fitted with a linear model:

$$\text{litter weight} = f(x) = b_1x + b_0$$

where x = litter size. As maximum litter size of yearling Dorset and Composite III ewes did not exceed twins, the linear model was fitted and these groups were not included in subsequent breed or age group comparisons for nonlinearity.

Analysis of variance was used to test homogeneity of quadratic regression coefficients among breeds. The model was litter weight = breed, litter size^2, litter size, breed × litter size^2, and breed × litter size, where litter size was fitted as a covariate (Table 2).

Efficacy of breed-specific quadratic equations to fit the data compared with a common quadratic equation was tested (Table 3). The test was based on the *F*-statistic:

$$F = \frac{(RSS_R - RSS_F)/(Rdf_R - Rdf_F)}{RSS_F/Rdf_F}$$

where RSS represents residual sum of squares and Rdf denotes residual degrees of freedom. The subscripted R denotes the reduced statistical model (common equation) and the subscripted F denotes the full statistical model (breed-specific equations). Data were analyzed separately by breed to calculate RSS specific to each breed. The same statistic was used to test homogeneity of equations between breeds with litter sizes of one to three lambs (Dorset and Rambouillet), one to four lambs (Suffolk and Composite III), or one to six lambs (Finnsheep and Romanov; Table 3). In a similar manner, yearling- and mature-specific equations were compared within Suffolk, Finnsheep, and Romanov breeds (Table 4).

Results

Mature Ewes

Litter weight increased with increased litter size for all breeds (Figure 1; $P < 0.001$). Quadratic terms for Rambouillet, Composite III, Suffolk, Finnsheep, and Romanov litters were negative and differed from zero ($P < 0.04$; Table 2). The quadratic term did not differ from zero for Dorset litters ($P = 0.12$; Table 2); therefore, the relationship of litter weight and litter size can be described by a linear equation:

$$f(x) = 3.48(\text{SE } 0.14)x + 2.40(\text{SE } 0.27);\ R^2 = 0.72$$

Breeds differed in the quadratic ($P < 0.001$) term used to describe litter weight as a function of litter size (Table 2).

Breed-specific quadratic equations fit data better than using a pooled equation across all breeds ($P < 0.05$; Table 3). Results of comparing breed-specific equations to a pooled equation within level of prolificacy were mixed. Separate equations described the relationship between litter weight and litter size better than a pooled equation for Dorset and Rambouillet litters (one to three lambs) as it did for Suffolk and Composite III litters (one to four lambs; Table 3). However, individual Finnsheep and Romanov equations were not different; the common equation was as follows:

$$f(x) = -0.1631(\text{SE } 0.0412)x^2 + 3.0496(\text{SE } 0.2552)x + 1.3626(\text{SE } 0.3776)$$

Yearling Ewes

Like mature ewes, litter birth weights of yearling ewes increased as litter size increased (Figure 2). Litter sizes for yearling Composite III and Dorset ewes did not exceed twins, so quadratic terms could not be fitted. Litter birth weight increased for Composite III:

Table 2. Relationship between litter birth weight (kg) and litter size ($f[x] = b_2x^2 + b_1x + b_0$) for mature and yearling ewes for each breed[a]

Age/breed	b_2[a]	SE	H_0: $b_2 = 0$[b]	b_1[a]	SE	b_0[a]	SE	R^2	Litter size
Mature ewes									
Dorset	–0.30[def]	0.20	0.124	4.6	0.7	1.5	0.6	0.72	1 to 3
Rambouillet	–0.82[de]	0.24	<0.001	6.5	0.8	0.2	0.6	0.79	1 to 3
Composite III[c]	–0.39[def]	0.14	0.005	5.4	0.5	1.3	0.5	0.62	1 to 4
Suffolk	–0.76[d]	0.13	<0.001	7.0	0.5	0.0	0.5	0.66	1 to 4
Finnsheep	–0.14[fg]	0.07	0.042	2.9	0.4	1.6	0.5	0.66	1 to 5
Romanov	–0.22[eg]	0.07	0.003	3.4	0.5	0.8	0.9	0.64	1 to 6
Yearling ewes									
Suffolk	–1.33[h]	0.43	0.002	7.0	1.4	–0.3	0.9	0.55	1 to 3
Finnsheep	–0.07[i]	0.08	0.388	2.2	0.3	1.6	0.3	0.64	1 to 4
Romanov	–0.32[hi]	0.17	0.070	3.5	0.9	0.4	1.1	0.65	1 to 4

[a]b_2 is the quadratic regression coefficient, b_1 is the linear regression coefficient, and b_0 is the intercept.
[b]Test that b_2 differs from zero.
[c]Composite III (a three-breed composite: ¼ Suffolk, ¼ Hampshire, ½ Columbia).
[d,e,f,g]Breed coefficients of mature ewes that do not have a common superscript letter differ ($P < 0.05$).
[h,i]Breed coefficients of yearling ewes that do not have a common superscript letter differ ($P < 0.05$).

$$f(x) = 3.43(\text{SE } 0.14)x + 2.49(\text{SE } 0.17);\ R^2 = 0.52$$

and Dorset ewes with increased litter size:

$$f(x) = 2.29(\text{SE } 0.29)x + 2.91(\text{SE } 0.33);\ R^2 = 0.34$$

Litter birth weight increased at a decreasing rate for Suffolk ewes ($P = 0.002$; Table 2); however, the quadratic term did not differ from zero for Finnsheep ($P = 0.39$) and Romanov litters ($P = 0.07$; Table 2). A linear equation described the increases in litter birth weight with increased litter size of Finnsheep yearling ewes:

$$f(x) = 1.95(\text{SE } 0.07)x + 1.78(\text{SE } 0.13);\ R^2 = 0.64$$

and Romanov yearling ewes:

$$f(x) = 1.96(\text{SE } 0.17)x + 2.15(\text{SE } 0.43);\ R^2 = 0.64$$

Age-specific quadratic equations fit the data better than pooled equations for Suffolk, Finnsheep, and Romanov ewes (Table 4).

Discussion

Litter birth weight increased at a decreasing rate in mature ewes for all breeds except the Dorset. Our study suggests that for Dorsets, litter birth weight increases linearly with increased litter size (one through three lambs). Whereas litter birth weight increased at a decreasing rate for mature Romanov and Finnsheep ewes, litter weights of yearling ewes of the same breeds in-

Table 3. Comparison of the fit of breed-specific functions compared to pooled functions between breeds that have similar ranges of litter size

Breeds	Litter sizes	Residual Sum of squares	Residual df	F[a]
Dorset	1 to 3	347	228	
Rambouillet	1 to 3	369	318	
Dorset + Rambouillet	1 to 3	738	549	5.70*
Suffolk	1 to 4	1,657	566	
Composite III[b]	1 to 4	2,171	681	
Suffolk + Composite III	1 to 4	3,860	1,250	3.49*
Finnsheep	1 to 5	683	394	
Romanov	1 to 6	436	194	
Finnsheep + Romanov	1 to 6	1,124	591	0.81
All breeds	1 to 6	10,997	2,396	149.51*

*$P < 0.05$.
[a]F-test of the hypothesis that breed-specific functions are equivalent.
[b]Composite III (a three-breed composite: ¼ Suffolk, ¼ Hampshire, ½ Columbia).

Table 4. Comparison of the fit of age specific functions compared to a pooled function within breeds

Breeds	Residual Sum of squares	Residual df	F[a]
Suffolk			
Yearling	413	310	
Mature	1,657	566	
Yearling + mature	2,526	879	64.41*
Finnsheep			
Yearling	399	434	
Mature	683	394	
Yearling + Mature	1,274	831	48.98*
Romanov			
Yearling	88	77	
Mature	436	194	
Yearling + mature	570	274	7.93*

*$P < 0.05$.
[a]F test of the hypothesis that age-specific functions are equivalent.

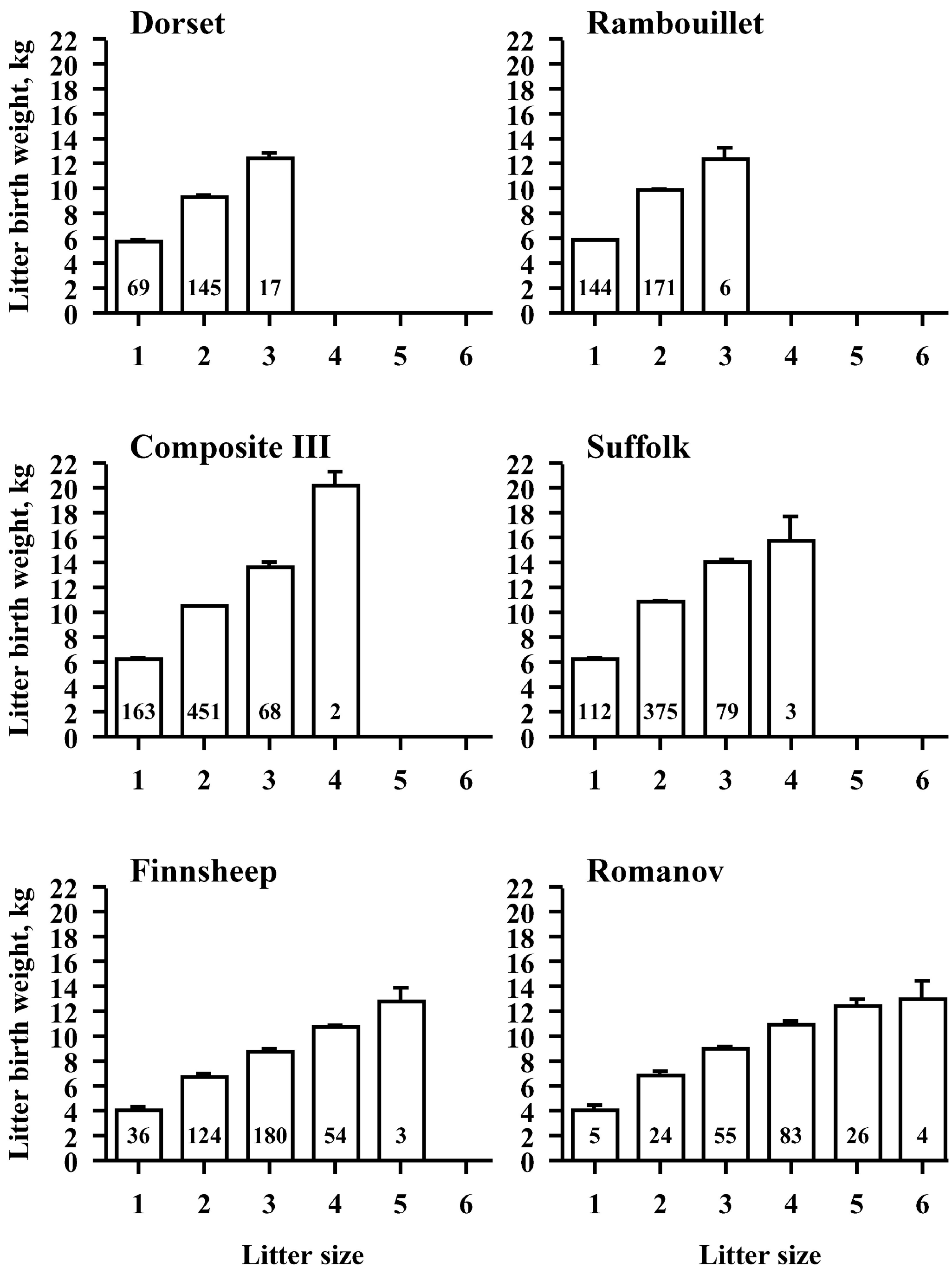

Figure 1. Mean (SE) birth weight of litters born to mature ewes (>34 mo). Values within bars are the total number of litters. Composite III (a three-breed composite: ¼ Suffolk, ¼ Hampshire, ½ Columbia).

creased linearly with increased litter size. The linear relationship of yearlings between litter birth weight and litter sizes may partially be a function of fewer lambs (one through four) in each litter compared to mature ewes (one through six). Over the same range of litter sizes observed in yearling ewes (one through four), we would reject that the quadratic term differed from zero for mature Romanov ($P = 0.07$) and Finnsheep ($P = 0.39$) ewes. Litter sizes in the Romanov and Finnsheep were larger than in the other breeds and the rate at which gains in litter birth weight decreased were in general lower than the other breeds (Table 2). This trend for a lower decrease in rate of gain of litter birth weight with increased litter size does not appear to be due simply to a reduction in litter birth weight compared with ewe BW (Figure 3), but rather a physiological adaptation that allows ewes to support a larger amount of fetal weight.

The relationship between litter birth weight and litter size differed among breeds. This difference most likely reflects differences among breeds in mature BW. Donald and Russell (1970) reported a positive relation-

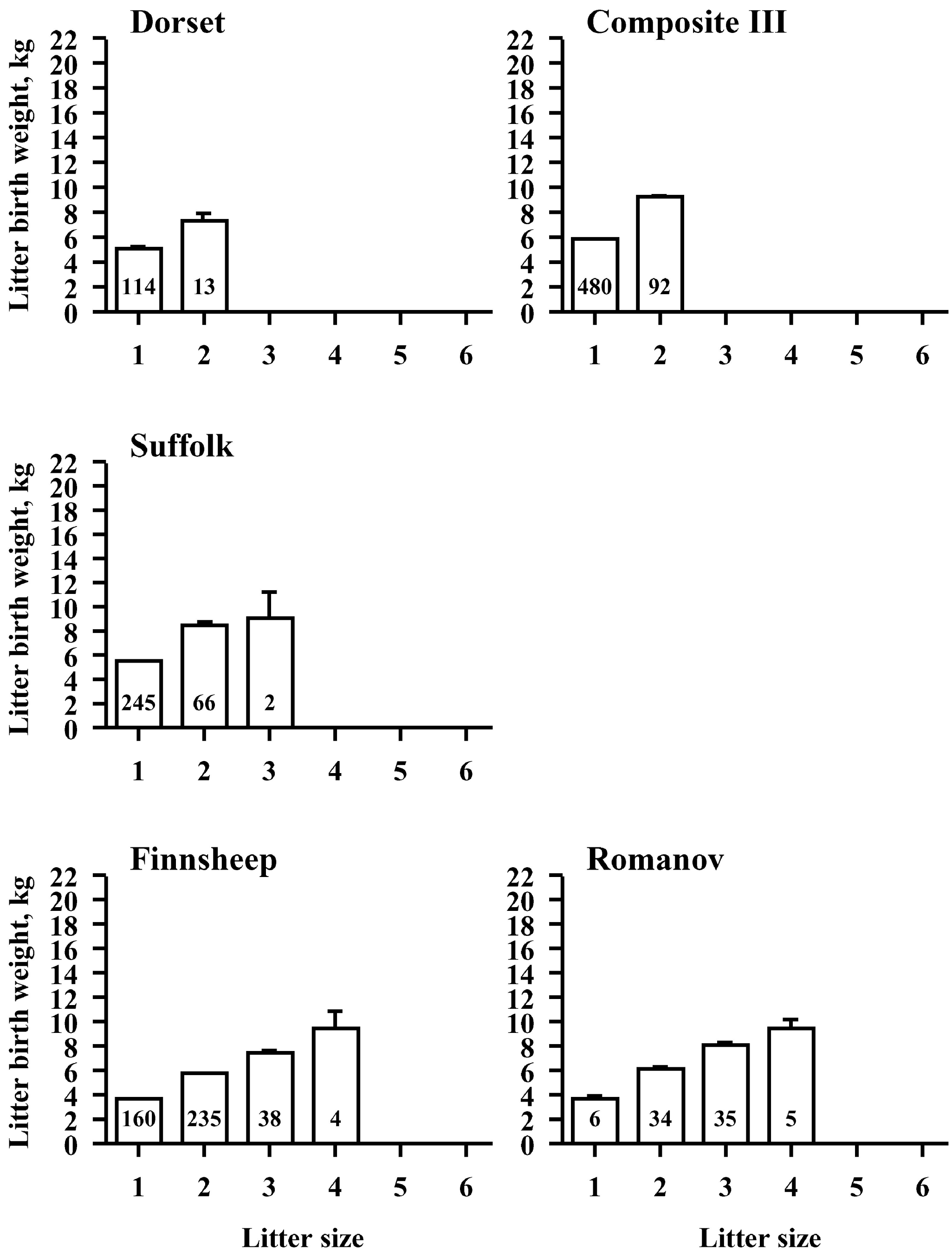

Figure 2. Mean (SE) birth weight of litters born to yearling ewes (11 to 15 mo). Values within bars are the total number of litters. Composite III (a three-breed composite: ¼ Suffolk, ¼ Hampshire, ½ Columbia).

ship between ewe BW at mating and litter birth weight. However, litter birth weight expressed as a proportion of the ewe's BW at mating decreased as ewe BW increased. In their study, the ratio of birth weight:mated ewe BW of single lambs ranged from 9.6% for light ewes to 6.5% for heavy ewes. Based on average breeding BW for the ewes in our study, we estimate a similar range in the ratio for single lambs (Figure 3). The maximum litter birth weight as a fraction of ewe BW ranged between 19 and 21%, regardless of litter size for breeds with lower prolificacy (≤4 lambs), but in breeds with higher prolificacy (>4 lambs), the ratio exceeded 24% (Figure 3). These differences in the ratio of litter birth weight to ewe BW suggest that breeds differ in the metabolic demand per unit BW during pregnancy and that nutrient models developed solely as a function of ewe BW during pregnancy may not reflect nutrient requirements.

Adjusting maternal nutrient recommendations for pregnancy will need to account for the curvilinear increase in litter birth weight with increased litter size. Nutrient flow to the gravid uterus increases as preg-

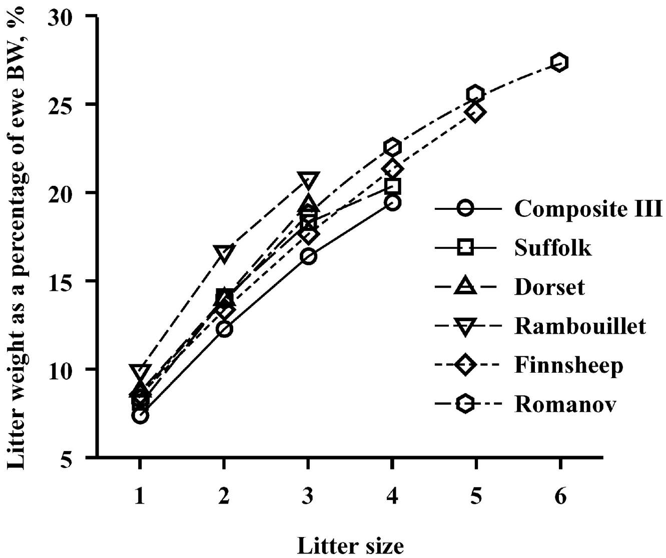

Figure 3. Litter birth weight expressed as a percentage of average ewe BW at breeding within breeds of mature, nonlactating, nonpregnant ewes. Composite III (a three-breed composite: ¼ Suffolk, ¼ Hampshire, ½ Columbia).

nancy advances (Meschia et al., 1980; Bell et al., 1986), and changes in maternal metabolism accompany the increase in nutrient flux to the gravid uterus (Freetly and Ferrell, 1998). In cattle, increases in fetal number result in an increase in nutrient flow to the gravid uterus (Ferrell and Reynolds, 1992), and in sheep, reductions in oxygen consumption per unit tissue of twin fetuses compared to single fetuses would be offset by increased total fetal weight of twin fetuses (James et al., 1972). Fitting fetal weight data to days of gestation with either a regression equation (Rattray et al., 1974) or a Gompertz equation (Robinson et al., 1977) predicts that litter size will start influencing measurable total fetal weight between 80 and 100 d of gestation. This stage of gestation is the same time that hepatic glucose release and lactate flux across the maternal liver begins to differentiate between ewes with single and twin fetuses (Freetly and Ferrell, 1998).

The ability of the ewe to provide sufficient nutrients to the gravid uterus influences the rate of fetal growth and subsequently birth weights. Environmental factors such as heat stress (Bell et al., 1987b) and maternal nutrient restriction (Chandler et al., 1985) decrease nutrient delivery to the gravid uterus and these environmental factors can decrease litter weights (Wallace, 1948). Birth weights of lambs from well-nourished ewes decrease as litter size increases, suggesting that reduced birth weight is not solely a function of maternal nutritional factors. The decreasing rate of increase in litter birth weight with increased litter size for these breeds of sheep suggests that fetal growth is increasingly restricted as litter size increases.

In the current study, individual birth weights decreased with increased litter size, suggesting that nutrient availability to the fetuses may become restricted with multiple fetuses. Nutrient availability to the fetus may result from either a reduction in available nutrients presented to the fetus (inadequate maternal nutrition) or a reduction in the delivery of nutrients to the fetus (placental transport). Umbilical blood flow to twin fetuses is lower than that to single fetuses in sheep (James et al., 1972) and cattle (Ferrell and Reynolds, 1992). Increasing litter size results in decreased cotyledon number, weight, and surface area (Kaulfub et al., 2000). McCoard et al. (2000) reported a reduction in both placentome number and weight, which resulted in a decrease in skeletal muscle hypertrophy during late gestation. Our findings are consistent with the theory that nutrient availability limits fetal growth as litter size increases and that models that account for nutrient availability are needed when predicting fetal growth in ewes that have multiple lambs per litter.

The hypothesis that litter weight will increase at a decreasing rate with increased litter size is largely supported, particularly for mature ewes. However, developing an across-breed mathematical predictor of litter birth weight will require more information than litter size due to breed differences in the rate by which this decrease occurs.

Implications

Nutrient recommendations for the pregnant ewe need to account for litter size as well as breed type. Development of robust predictors of nutrient requirements during pregnancy that can be used across breeds may require a more mechanistic approach than calculating recommendations as a function of body weight.

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